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Review

Social regulation of reproduction in male cichlid fishes

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ABSTRACT

Social interactions and relative positions within a dominance hierarchy have helped shape the evolution of reproduction in many animals. Since reproduction is crucial in all animals, and rank typically regulates access to reproductive opportunities, understanding the mechanisms that regulate socially-induced reproductive processes is extremely important. How does position in a dominance hierarchy impact an individual's reproductive behavior, morphology, and physiology? Teleost fishes, and cichlids in particular, are ideally-suited models for studying how social status influences reproduction on multiple levels of biological organization. Here I review the current knowledge on the reproductive behavioral and physiological consequences of relative position in a dominance hierarchy, with a particular focus on male cichlids. Dominant and subordinate social status is typically associated with distinct differences in activity along the entire hypothalamic–pituitary–gonadal axis. Further, when transitions in social status occur between subordinate and dominant individuals, there are plastic changes from whole-organism behavior to molecular-level gene expression modifications that occur quickly. These rapid changes in behavior and physiology have allowed cichlids the flexibility to adapt to and thrive in their often dynamic physical and social environments. Studies in cichlid fishes have, and will continue, to advance our understanding of how the social environment can modulate molecular, cellular, and behavioral outcomes relevant to reproductive success. Future studies that take advantage of the extreme diversity in mating systems, reproductive tactics, and parental care strategies within the cichlid group will help generate hypotheses and careful experimental tests on the mechanisms governing the social control of reproduction in many vertebrates.

1. Introduction

In social animals, relative position in an established dominance hierarchy has important consequences for health, survival, and reproductive fitness (Sapolsky, 2005; Wingfield and Sapolsky, 2003). Dominance status in fishes may be influenced by several factors including relative body size or age, territory availability and quality, nutritional state and body condition, or overall group composition. Dominance is typically decided, however, by repeated agonistic interactions between individuals resulting in a consistent winner that is perceived by all members of the social group. Since hierarchical position is crucial for survival and reproduction, many animals, including cichlid fishes, have evolved the ability to predict their own position in the society, as well as the relative social rank of others, through observation and transitive inference (Grosenick et al., 2007). Further, since environmental and social conditions are often dynamic, changes in an individual's relative social status can occur quickly and frequently within a population. How does an individual's social position influence his physiology and chances for reproduction? Cichlid fishes have become important model organisms for addressing this and related questions to further our understanding of the cellular and molecular mechanisms that regulate maintenance of social status positions in vertebrates.

Social rank can have profound impacts on an individual's reproductive behavior and physiology. In most cases, dominance is associated with increased reproductive opportunities, improved fitness, and an up-regulated reproductive axis compared to subordinate individuals. Notably, the influence of social rank has effects at every level of the reproductive axis from the brain to the testes, and at multiple levels of biological organization from whole animal behavior to molecular-level changes in gene expression (Maruska and Fernald, 2011b). In the sections below, I will review what is currently known about how social rank impacts reproductive behavior and physiology in male cichlids. I will focus primarily on the African cichlid *Astatotilapia burtoni*, an important and

Abbreviations: ATn, anterior tuberal nucleus; Ce, cerebellum; Dl, lateral part of the dorsal telencephalon; POA, preoptic area; Vs, supracommissural nucleus of the ventral telencephalon; VTn, ventral tuberal nucleus; Vv, ventral nucleus of the ventral telencephalon.

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emerging model system for studying the social control of reproduction (Fig. 1), and make comparisons to other cichlid species where information is available. *A. burtoni* is a maternal mouthbrooding cichlid endemic to Lake Tanganyika, Africa. Males of this species exist in two different phenotypes: dominant territorial males comprise ~10–30% of the population, are brightly colored, and aggressively defend a territory that serves as a food and spawning resource; and subordinate non-territorial males that

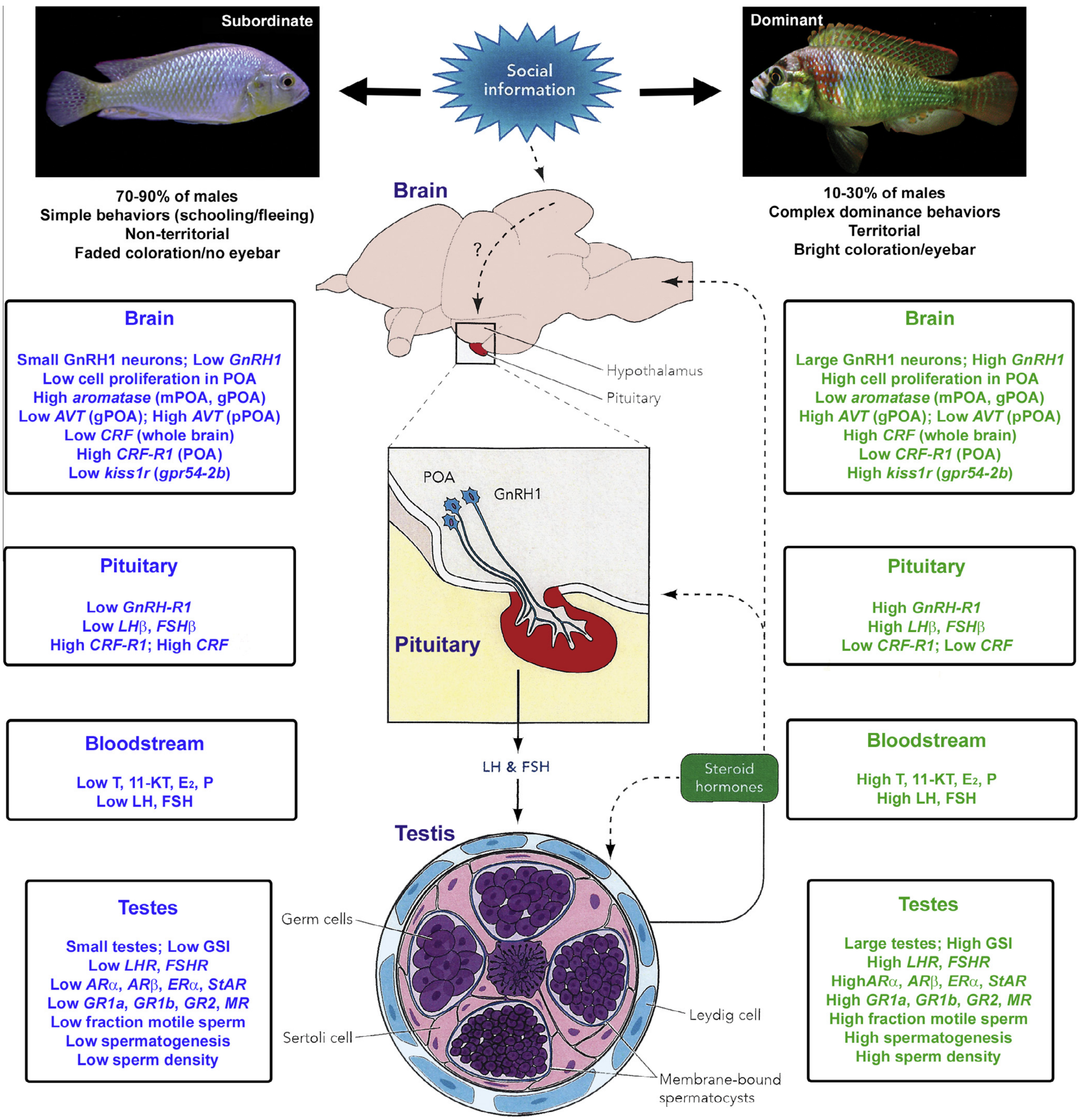

Fig. 1. Summary of social status differences in the hypothalamic–pituitary–gonadal (HPG) axis between dominant and subordinate male *Astatotilapia burtoni*. Dominant males (right) are brightly-colored, defend a territory, and exhibit many territorial and reproductive behaviors, while subordinate males (left), have more faded coloration similar to females, do not hold territories, and display submissive behaviors. Dominant males also have an up-regulated HPG axis compared to subordinate males. The HPG axis is also influenced by the social environment, and can rapidly change when males transition between lower-ranking and higher-ranking status, in both directions. Only those measures directly relevant to the HPG axis and reproduction are shown. Italicized genes indicate mRNA levels quantified via qPCR or *in situ* hybridization. Modified in part from Maruska and Fernald (2011b, 2013b) and data were compiled from the following studies (Carpenter et al., 2014; Chen and Fernald, 2006; Davis and Fernald, 1990; Greenwood et al., 2008; Grone et al., 2010; Huffman et al., 2012, 2013; Kustan et al., 2012; Maruska et al., 2012a, 2011, 2013b; Maruska and Fernald, 2010a, 2011a; O'Connell et al., 2013). *Abbreviations*: 11-KT, 11-ketotesosterone; ARα, ARβ, androgen receptor subtypes α and β; AVT, arginine vasotocin; CRF, corticotropin-releasing factor; CRF-R1, CRF receptor 1; E_2, 17ß-estradiol; ERα, estrogen receptor subtype α; FSHβ, β-subunit of follicle stimulating hormone; FSHR, FSH receptor; GnRH1, gonadotropin releasing hormone 1; GnRH-R1, GnRH receptor subtype 1; gPOA, gigantocellular POA; GR1a, GR1b, GR2, glucocorticoid receptor subtypes 1a, 1b, 2; kiss1r, kisspeptin receptor 1 (gpr54-2b), LHβ, β-subunit of luteinizing hormone; LHR, LH receptor; mPOA, magnocellular POA; MR, mineralocorticoid receptor; P, progesterone; POA, preoptic area; pPOA, parvocellular POA; StAR, steroidogenic acute regulatory protein; T, testosterone.